18. On some new Therocephalian Reptiles from the Karroo Beds of South Africa. By R. Broom, M.D., D.Sc., F.R.S., C.M.Z.S.

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(Text-figures 1–9.)

Index.

Though more species and genera of Therocephalians are known than of either of the other two large suborders of the Carnivorous Therapsida—the Gorgonopsia and the Cynodontia,—the structure of the skull and skeleton is much better known in these later suborders. This is largely due to the fact that the Therocephalians are mainly found in the Lower Beaufort zones, where, owing to the petrological conditions, very fine complete specimens are rare. The Gorgonopsians which are found mostly in the *Cistecephalus* zone, and the Cynodonts which mainly occur in the Upper Triassic zones, are usually represented by well-preserved skulls with a matrix which can be fairly easily removed. Recently I have been fortunate in discovering one or two very interesting specimens of late Therocephalians formed in the Upper *Endothiodon* and *Cestecephalus* zones, which add considerably to our knowledge of the Therocephalian skull.

Ictidosuchus longiceps, sp. nov.

In 1900 I discovered near Pearston the remains of a very interesting type of Therocephalian which I described under the name *Ictidosuchus primævus*. Until recently no other specimen of either this genus or species has ever been discovered, and as the type skull is very imperfect, a good specimen of this genus has long been one of our principal desiderata. In December 1917, I found at Bruintjeshooyte, between Somerset East and Pearston, a good skull, which may be referred to the genus *Ictidosuchus*, though a distinct species from *I. primævus*.

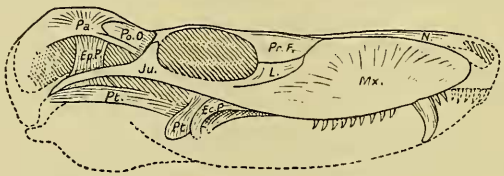
The skull is nearly complete, lacking only the incisor portion, the occipital condyle, the arches of the left side and the quadrate region of the right. The palate is much weathered on the left side, but nearly perfect on the right.

As preserved, the skull measures in greatest length 135 mm., and when complete was probably 152 mm. long. The greatest breadth is about 84 mm. From the front of the orbit to the base of the canine is 52 mm., and from the front of the orbit to

the front of the snout was probably about 75 mm. The interorbital measurement is 22 mm., and the antero-posterior measurement of the orbit is 32 mm.

The premaxillæ and septomaxillæ are lost. The nasals are long and narrow, only slightly wider in front and behind than in the middle region. The maxilla is unusually long in comparison with its depth. It passes forwards a considerable distance in advance of the canine and backwards much beyond the last molar. In front of the main canine there are two small canines as in *Scaloposaurus*, but the present type, besides differing very greatly in many other ways, differs in having the third tooth developed into a powerful canine. The canine here measures about 15 mm. in height and 5 mm. in antero-posterior length. It is usually curved, and is remarkable for having no serrations along its posterior border. The three canines together measure 9·5 mm. Behind the main canine is a diastema of 6·5 mm. followed by a series of 9 small cone-like molars, the whole molar series measuring 25 mm. In *Ictidosuchus primævus* there are apparently only 8 molars, but as both the upper and lower jaws are

Text-figure 1.*



Side view of skull of *Ictidosuchus longiceps* Broom.

badly preserved, it is not improbable that there may also have been 9 in the type species. The molars of *Ictidosuchus primævus* are considerably larger and closer together, but appear to be otherwise similar to those of *I. longiceps*.

The prefrontal is a relatively large bone which forms the anterior half of the upper orbital margin and extends down to the middle of the anterior border. The lacrimal is considerably less than half the size of the prefrontal, as will be seen in the figure given.

The jugal is a very long slender bone forming most of the suborbital bar and about half of the outer temporal arch. A strong but short ascending process forms the lower half of the postorbital arch, articulating with the short postorbital bar of the postorbital bone.

The frontals are relatively small, and only form a very small part of the supraorbital margin. The bones are about the same length as the orbit, and articulate in front with the nasals by

* For explanation of lettering, see p. 355.

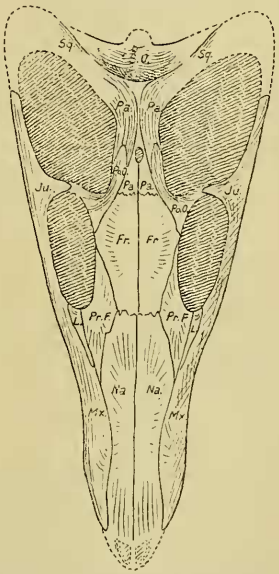
an irregular transverse suture, and posteriorly with the parietals by a transverse serrated suture.

There is no postfrontal.

The postorbital is relatively small, forming the posterior half of the upper orbital margin and the upper half of the postorbital arch. It extends backwards by the side of the parietal to the plane of the posterior border of the pineal foramen.

The parietals are relatively long and slender. In front they are flattened out, and form a transverse suture with the frontals. Posteriorly they form a sharp intertemporal crest, and at the front of the crest is a large oval pineal foramen. From the

Text-figure 2.



Upper surface of skull of *Ictidosuchus longiceps* Broom.

posterior part of the crest the parietals pass outwards, forming a considerable part of the occipital crest.

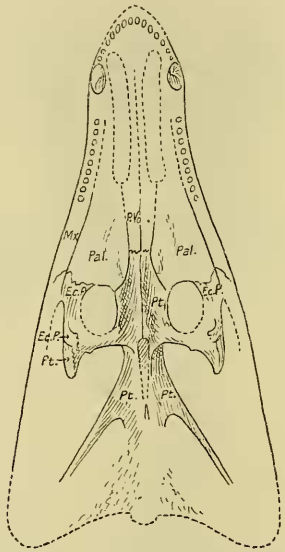
The occiput is very imperfectly preserved. It is shallow and broad, and from the upper margin of the foramen magnum the bone passes upwards and forwards. The elements cannot be clearly made out, though they are doubtless as in better-known Therocephalians. The squamosals and quadrates are lost.

As already stated, the palate has not been fully cleared in front as the matrix is required to support the teeth, but the structure is sufficiently revealed in all the posterior part. A transverse fracture through about the plane of the third last molar shows in section the prevomers. Though very closely placed to each other

they are not anchylosed. Each has an ascending thin plate and a short descending plate, and from each bone a transverse plate passes outwards which approaches and doubtless further back meets the palatine. The palatines as seen here in section are slender curved bones which below meet the maxillaries, and on passing inwards and then upwards again approach and possibly meet the upper borders of the maxillaries.

The prevomers extend backwards a considerable distance behind the plane of the last molars and meet the anterior ends of the pterygoids. The palatines form the greater part of the bony roof of the mouth, passing about as far back as the posterior end

Text-figure 3.



Palatal surface of skull of *Ictidosuchus longiceps* Broom.

of the maxilla. There is behind the palatine a large suborbital vacuity as in *Scylacosaurus*, and, as in that genus, this vacuity is bounded externally by the ectopterygoid. The ectopterygoid is moderately slender, but in front of the pterygoid process which lies along the inner side of the mandibles it has a well-developed descending process, which adds much support to the pterygoid process.

The pterygoid is fairly similar to that already described and figured by me in *Scylacosaurus*, and possibly some of the apparent differences may be due to certain features being preserved in the present specimen which were lost in the other. As in most primitive reptiles, there is an anterior process which, passing

inside of the palatine, meets the prevomer; an outer descending process which forms the posterior border of the suborbital vacuity and has a long articulation with the ectopterygoid; and a long posterior process, the inner part of which apparently articulates with the basisphenoid, and the outer branch of which doubtless passes back to meet the quadrate. Though the posterior process is almost perfectly preserved, as the quadrate is lost the mode of articulation is not seen. An interesting point about the pterygoid is that there are no teeth on it. Near the posterior part of the anterior palatine process there is in the middle line a prominent median spur formed by the two bones meeting, and immediately behind this is a moderately large median vacuity. At the inner end of the outer process is a well-marked descending spur, the exact length of which is unknown as it is broken off near the base.

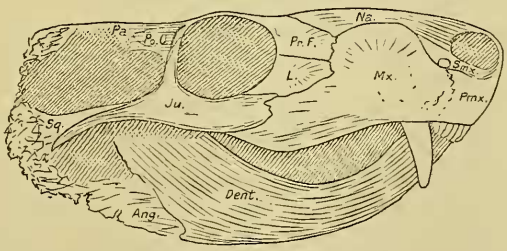
Above the outer branch of the posterior process is seen the well-developed epipterygoid. This differs from that figured by me in *Scylacosaurus* (Phil. Trans. 1915) in having a shorter and broader upper portion and a differently shaped basal, which lies in the pterygoid as seen in the figure given.

The basicranial region is too much weathered to be worth describing in detail.

Alopecopsis atavus, gen. et sp. nov.

This new genus and species is founded on a nearly complete skull discovered by me at New Bethesda, and it is of much importance as revealing another new type of Therocephalian.

Text-figure 4.



Side view of skull of *Alopecopsis atavus* Broom.

The specimen is in rather indurated shale, and as the bone is more friable than the matrix, complete development is difficult, and it has been considered advisable to leave a fair amount of matrix on the specimen. Enough has, however, been undertaken to show most details of the structure. The whole of the right side of the skull is preserved except a part of the quadrate and squamosal regions, and the right mandible is in position. The left side has lost the greater part of the jugal and squamosal,

and the left mandible has been completely detached and lost before fossilisation.

The skull as preserved measures 198 mm. and was probably about 202 mm. in greatest length. The greatest width across the squamosals has been about 90 mm. From the front of the snout to the front of the orbit is 90 mm. The greatest width of the snout in the canine region is 45 mm., and the narrowest measurement between the supraorbital edges is 39 mm.

The premaxilla is relatively small, and is much overlapped by the maxilla. It sends upwards between the nostrils a slender internasal process to meet the nasal above. Most of the teeth are lost, but portions of three are stil seen, and from the sockets the number and size of all can be determined. There is evidence of six incisors, of which the 6th is very small. The whole six measure 24 mm. At the front end of the premaxilla are two moderately large foramina for branches of sensory nerve—presumably a branch of the second division of the Vth.

The septomaxilla lies along the outer border of the nostril, and passes backwards a short distance between the nasal and maxilla. Between the septomaxilla and maxilla there is, as in other previously known early carnivorous Therapsids, a large foramen, the significance of which is at present unknown. In most fœtal mammals there is a large gland duct developed along the outer side of the nasal cavity, which from its very early development is evidently the remains of some structure once of much greater importance. It seems not improbable that this large foramen, which passes into the nasal cavity between the septomaxilla and maxilla and is continued as a wide groove for some distance upwards and backwards along the upper border of the maxilla, was for the lodgment of the glandular and possibly sensory organ whose rudiment is met with in most mammals.

The nasal is long and narrow, but broader at each end than in the middle. The shape and relations will be best understood from the figures given.

The maxilla is a powerfully developed bone of considerable depth. There is a single large canine which unfortunately is not well preserved on either side. In front of the elevation which accommodates the root of the canine, the maxilla overlaps the premaxilla as in most Therocephalians, and in the anterior part of the bone are three fairly large foramina, presumably for branches of the Vth nerve. In the canine region the surface of the bone is considerably pitted, probably by glands in the skin, and there are a number of small openings, apparently for nerves. The maxillary branch of the Vth nerve apparently passes into the maxilla by a large foramen on the inner side of the bone behind the canine, and passing forwards outside the canine, comes to the surface through the numerous small foramina in the front of the bone. Behind the canine there is a long slender alveolar margin, which is remarkable in having no trace of molar

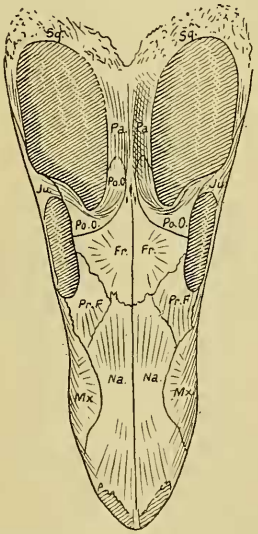
teeth. In many skulls when no molars are found we suspect that they may have been lost, but here this can hardly be the case. Both maxillæ are well preserved and the dentary as well, yet in none of the three bones is there any trace of molars. Further, the alveolar margin is narrow and sharp, and would be much too slender for the accommodation of molars large enough to be serviceable to an animal of the size.

The lacrimal is fairly large, and forms a considerable part of the facial surface, which is very smooth.

The prefrontal forms the anterior and upper quarter of the orbital margin. It meets the frontal, nasal, maxilla, and lacrimal bones.

The frontals are relatively small, and the two form most of the

Text-figure 5.



Upper surface of skull of *Alopecopsis atavus* Broom.

slightly concave interorbital surface. In front each has a short articulation with the nasal and a much longer oblique articulation with the prefrontal, and as the prefrontal nearly extends backwards to the postorbital, the frontal only forms a very small part of the orbital margin. Posteriorly the frontal has a long articulation with the postorbital, and a short interdigitating suture with the parietal mainly hidden by the postorbital.

There is no postfrontal.

The postorbital is a peculiarly twisted bone. Its inner end lies against the narrow parietal crest, and from this, passing

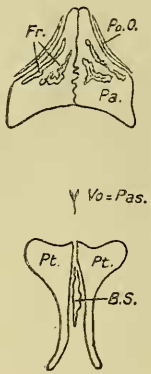
outwards, it forms the back wall of the frontal region and the anterior border of the temporal fossa. From the point where it meets the frontal at the orbital margin it passes almost directly backwards, forming most of the posterior half of the upper orbital margin. It then passes downwards behind the jugal to nearly the level of the lower side of the orbit.

The jugal is a large bone. It forms almost the whole of the suborbital arch and about half of the postorbital. Posteriorly it passes back below the squamosal to near the quadrate region.

The parietals are narrow, and form a median crest which in front is overlapped by the postorbitals. The pineal foramen is rudimentary.

The back of the skull is not well preserved, the bones being very rotten, but so far as can be seen the structure does not differ from that of typical Therocephalians.

Text-figure 6.



Section through skull of *Alopecopsis atavus* Broom, immediately behind postorbital arch.

A section through the skull immediately behind the post-orbital arch shows the relations of the parietals and postorbitals above and the pterygoid below, with between them a thin anterior process of the basisphenoid, and above them the feebly developed element which I believe to be the true vomer, but which most others call the parasphenoid.

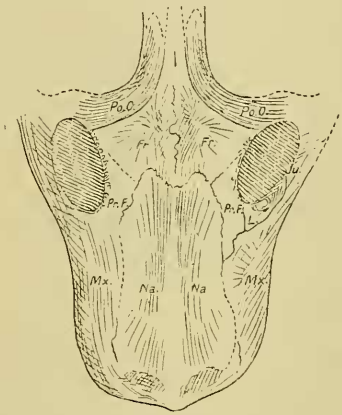
The right mandible is fairly complete and the dentary almost perfect. In front there are three incisors which together measure 9 mm., and these are closely followed by a long procumbent canine which has antero-posterior diameter of 8·5 mm. and a height of something over 20 mm. There appear to be no serrations on either the incisors or the canine. Though the alveolar margin of the dentary is perfectly preserved, there is no trace to be seen of any

molars. The dental formula of *Alopecopsis atavus* is thus the very remarkable one :—i. $\frac{6}{3}$, c. $\frac{1}{1}$, m. $\frac{0}{0}=\frac{7}{4}$. As will be seen from the figure I give, the dentary is very peculiarly shaped. Behind the canine the upper border of the bone is deeply concave, so that, even if there had been teeth, they could not have met molars in the upper jaw unless they were exceptionally long. The back part of the dentary is powerful, and there is a long but thick coronoid process. The coronoid bone is well developed, not so deep as and much thicker than the coronoid in Gorgonopsians or Cynodonts. The back part of the jaw is not sufficiently well preserved to admit of description, but it is relatively much shorter than in Gorgonopsians and apparently more like that of *Bauria*.

Moschorhinus kitchingi, gen. et sp. nov.

This new genus and species is founded on a well-preserved specimen discovered by Mr. James Kitching near New Bethesda Road. It consists of the anterior two-thirds of the skull of

Text-figure 7.



Upper surface of front of skull of *Moschorhinus kitchingi* Broom.

a moderately large Therocephalian. The specimen is slightly crushed, but the matrix is only slightly harder than the bone, and it has been found possible to display almost every detail of the structure of the palate.

The skull is manifestly that of a broad-headed short-snouted form, the front of the snout being usually blunt and wide.

The premaxillaries are broad and powerful, and each carried six well-developed incisors. As preserved, each bone has only five teeth, but quite manifestly the 3rd is lost from the right side and the 6th from the left. The whole series measures 41 mm. The first four incisors are much flattened and with the long axis

directed mainly antero-posteriorly. The posterior two incisors are more rounded.

The septomaxillary is large, and forms the lower border of the nostril, but does not extend far backwards between the nasal and the maxilla. The foramen, usually present between the septomaxilla and maxilla, is small.

The nasal bone is exceptionally large and broad. In front it is crushed down on the nostrils and the details of structure cannot be made out, but doubtless the arrangement is similar to that in typical Therocephalians. Posteriorly the nasal meets the frontal a little in front of the plane through the centre of the orbit. The shape of the bone will be best understood from the figure.

The maxilla is a short but powerful bone. It overlaps the premaxilla to between the roots of the 3rd and 4th incisors. It has one large canine which measures 26 mm. × 12 mm. Behind the canine only a very small part of the maxilla shows on the palatal aspect, and in the specimen there are no teeth, but on each side there are indications of two old sockets with a possible third very small one; and I think we may assume that there were three molars, of which the 3rd was small. The three would measure about 19 mm. The upper dental formula would thus be $i.^{6}$, $c.^{1}$, $m.^{3}$

The prefrontal is relatively small, and wedged in between the nasal and frontal above and the maxilla and lacrimal below.

The lacrimal is slightly larger than the prefrontal, and it forms most of the front of the orbit. Near the middle of the bone and on the orbital margin is a well-developed bony boss, and on the inner side of this and near its upper end is a large lacrimal foramen.

Very little of the jugal is preserved, but the part underneath the orbit forms with the maxilla a very deep and powerful suborbital arch.

The frontals are large and wide, as seen in the figure.

There is no postfrontal. The postorbital lies on the frontal and parietal.

The parietal crest is narrow as in typical Therocephalians, but the pineal foramen is rudimentary.

The palate is beautifully preserved and remarkably interesting. The palatal portion of the premaxillaries has not been displayed as the matrix is required to support the fragmentary incisors.

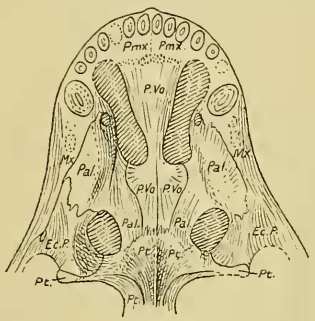
The prevomers form a large part of the bony roof of the mouth. In front they are anchylosed and form a wide plate between the internal nares. At the back part of the nares they are much constricted, but beyond this widen out again into a fan-shaped structure which lies between the palatines and meets the pterygoids. In this back part a median suture between the two prevomers is very distinctly seen.

The palatine is a large and powerful bone. Externally it has a long articulation with the maxilla, and here the palatine is so thickened that it forms more of the wide alveolar surface than does the maxilla. In front and nearly on the plane of the back of

the canine, where the maxilla passes up to form the vault of the palate, the palatine lies closely against the maxilla except where there is a large foramen, presumably for a nerve. Haughton figures two foramina in a corresponding structure in *Akidognathus*. Near the middle of the palatine is an oblique ridge, which probably supported a soft palate and carried the internal nares back to the anterior pterygoid region. The inner side of the palatine articulates with the prevomer and the pterygoid. The greater part of the posterior border forms the margin of the suborbital vacuity. Further out is a moderately large articulation with the ectopterygoid.

The ectopterygoid is an irregularly shaped bone, not unlike a bird's quadrate. Anteriorly it articulates with the palatine; externally with the maxilla and probably with the jugal. Between the maxilla and the ectopterygoid is a small foramen. Posteriorly there is a large flat articulation between the ectopterygoid and the pterygoid. In front of the pterygoid process there is an even larger ectopterygoid process. All the outer side

Text-figure 8.



Palate of *Moschorhinus kitchingi* Broom.

of the suborbital vacuity is formed by the ectopterygoid and much of the posterior.

Only the anterior portions of the pterygoids are preserved. From the broad deep lateral portions which articulate with the ectopterygoids they pass forward only a comparatively short distance to meet the prevomers and the palatines. In this region each pterygoid sends down a thin vertical plate, which, uniting with its neighbour, forms a median keel.

In general structure the palate agrees more closely with that in *Akidognathus*, though the proportions of the bones are very different. In *Akidognathus* the prevomers have, as in *Moschorhinus*, a suture between them, and yet are anchylosed in front. *Moschorhinus* differs in having no interpterygoid vacuity so far as can be seen in the specimen. If one be present, it must be much further back than in *Akidognathus*.

There is another palate recently discovered with which a comparison may be made—viz., *Whaitsia platyceps*. This new type was recently described by Haughton, and though it differs greatly from *Moschorhinus*, the snout has so much superficial resemblance that a comparison seems advisable, even if only to clearly differentiate the types. *Whaitsia* is a large Therocephalian—one of the largest known. It has a broad flat snout, and if it were not for the great difference in the palate, one might be inclined to think that *Moschorhinus* was a near ally. Further, in the type of *Whaitsia* the number of incisors cannot be made out, though there are four in what is regarded as a co-type. The palate, however, is so very unlike that of any form previously known

Text-figure 9.

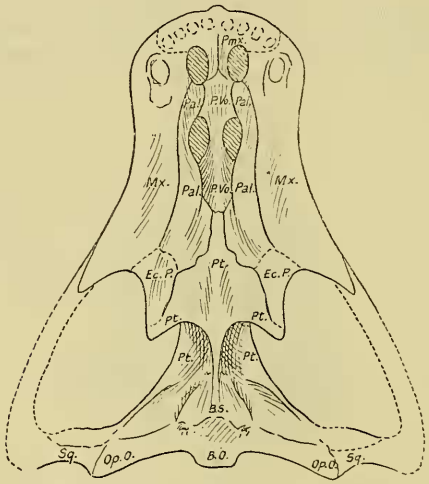


Diagram of palate of *Whaitsia platyceps* Haughton.

that Mr. Haughton very wisely puts *Whaitsia* in a new family—the Whaitsidiæ.

Mr. Haughton has given an excellent description of the type and a figure of both upper and lower sides. The description he has given is so accurate that little need be added to it. But the figure he gives of the palate is not very clear, and a new and independent figure of this unique palate may not be regarded as superfluous.

If the palate, as I figure it, be compared with that of *Moschorhinus*, it will be seen to differ in only two important points. The suborbital vacuity, which in all typical Therocephalians is large, is here practically closed, and the back part of the palate is thus made to resemble slightly that of the Gorgonopsia. In front, instead of there being a pair of large openings as in all

other known Therocephalians, there are four openings. If the anterior part of the palate be compared with that in *Moschorhinus*, it will be seen that the difference is that the anterior ends of the palatines pass inwards, and meet the prevomers dividing what were large internal nares into anterior and posterior portions—the posterior alone being, as Haughton has suggested, the internal nares. What has happened is exactly comparable to what has happened with the external nares in *Chamæleon*, where the original opening becomes divided into two by the prefrontal passing forwards.

Haughton discusses the affinities of *Whaitsia* with Therocephalians, Gorgonopsians, and Cynodonts, and inclines to regard it as a highly specialised Gorgonopsian, but it seems to me that it is a true but aberrant Therocephalian.

References to lettering.

Ang. Angular; *B.O.* Basioccipital; *B.S.* Basisphenoid; *Dent.* Dentary; *Ec.P.* Ectopterygoid or Transpalatine; *Ep.P.* Epipterygoid; *Fr.* Frontal; *Ju.* Jugal; *Mx.* Maxilla; *Na.* Nasal; *OpO.* Opisthotic or Paroccipital; *Pa.* Parietal; *Pal.* Palatine; *Pmx.* Premaxilla; *PrF.* Prefrontal; *PoO.* Postorbital; *Pt.* Pterygoid; *P.Vo.* Prevomer; *Smx.* Septomaxilla; *Sq.* Squamosal; *Vo=Pa.S.* Vomer=Parasphenoid.